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Is there a substitution of Pinaceae by Fagaceae in temperate forests at the global scale?

Teresa Alfaro Reyna[a], Javier Retana[a,b], Jordi Martínez-Vilalta[a,b,*]

[a] CREAF, Cerdanyola del Vallès, E-08193 Barcelona, Spain
[b] Univ. Autònoma Barcelona, Cerdanyola del Vallès, E-08193 Barcelona, Spain

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ABSTRACT

Reports on forest decline, changes in species composition and the distribution of forests in response to changes in climate and land use are increasing worldwide. Temperate forests are largely dominated by two tree families: Pinaceae and Fagaceae. These two families have distinct functional properties and different responses to environmental factors. Several local and regional assessments, particularly in Europe, have found that species of Fagaceae are invading areas previously dominated by Pinaceae. The main aim of this synthesis study is to analyze the relative dynamics of Pinaceae and Fagaceae species in temperate forests around the world, with the following specific objectives: (1) establish if there is a consistent directional substitution of Pinaceae by Fagaceae worldwide; and (2) determine whether these directional changes are associated with specific climatic conditions or certain geographic regions, reflecting differences in historical forest management and land use. A bibliographic review was performed and 51 papers were found that met the search criteria, including a total of 121 case studies in which the relative dynamics of Pinaceae and Fagaceae were evaluated. Our results show that the relative abundance of Fagaceae increased in 71% of cases (P → F dynamics), whereas Pinaceae relative abundance increased in 17% of cases (F → P) and 12% of cases did not show clear changes. Increases of Fagaceae relative to Pinaceae were less clear in areas where vegetation dynamics were driven by natural disturbances. Our results indicate a widespread increase in dominance of Fagaceae species at the expense of Pinaceae across northern temperate forests, with the exception of Eastern North America. The potential implications for ecosystem function and forest resilience under ongoing climate change are large and clearly deserve further study.

1. Introduction

There is an increasing number of studies reporting episodes of forest decline worldwide associated to climatic extremes (Allen et al., 2010; Reyer et al., 2015; Trumbore et al., 2015). This climatic signal, however, is usually difficult to separate from other drivers of forest change, particularly past changes in forest management and land use (e.g., Vayreda et al., 2016), as most of the world's forests have been extensively modified by human intervention. The interactions between climate change and land use changes may modify disturbance regimes and alter forest structure and functionality. Important disturbances, including drought, fire, and insect and pathogen outbreaks, may interact with each other causing cascading effects (Dale et al., 2001; Thompson et al., 2009). The compounded effects of disturbances can lead to new ecosystem states, resulting in changes in dominant species (Bahamondez and Thompson, 2016; Torres et al., 2016; but see Martínez-Vilalta and Lloret, 2016). A new state may be entered, for instance, when the system has not recovered from the first disturbance before a second perturbation occurs, leading to a new, long-term condition (Paine et al., 1998).

Temperate forests account for 26% of forest area worldwide (Keenan et al., 2015; Riitters et al., 2016) and cover large areas of the northern hemisphere, dominating mid-latitudes in North America, Asia, and Europe (Olson et al., 2001). This biome is dominated by deciduous broadleaf trees and evergreen conifers, mostly belonging to two families: Fagaceae (angiosperm) and Pinaceae (gymnosperm) (Woodward et al., 2004). Despite substantial ecological differences, these two families can coexist in large areas characterized by distinct seasonality, including a marked dry season in some regions (Manos and Stanford, 2001; Eckenwalder, 2009). Pinaceae is a diverse conifer family with 11 genera and 225 species (Christenhusz et al., 2011). The genus *Pinus* is the most diverse and abundant of the family, and comprises approximately 110 species (Eckenwalder, 2009). Fagaceae is represented by eight genera and about 927 species (Christenhusz and Byng, 2016). *Quercus* is the most diverse genus within the family, consisting of over 500 species and having a great ecological and economic importance

* Corresponding author at: CREAF, Campus UAB, Edifici C, Cerdanyola del Vallès, E-08193 Barcelona, Spain.
E-mail addresses: alfaro.teresa@inifap.gob.mx (T. Alfaro Reyna), Javier.Retana@uab.cat (J. Retana), Jordi.Martinez.Vilalta@uab.cat (J. Martínez-Vilalta).

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(Nixon, 2006).

It has been hypothesized that conifers in general, and Pinaceae in particular, are largely restricted to areas where growth of angiosperm competitors is reduced, such as high latitudes and elevations (cold environments) or nutrient-poor soils (Bond, 1989). However, this paradigm does not seem to explain contemporary forest dynamics in some regions, where Pinaceae have been aggressive competitors capable of dominating entire regions, often to the exclusion of angiosperm trees (Brodribb et al., 2012). Pinaceae species are well adapted to freezing, thanks mostly to their wood anatomy (small xylem conduits highly resistant to freeze-thaw embolism) and their leaf morphology and photosynthetic physiology. Conifers, however, can also sustain maximum photosynthetic rates that are similar or even higher than those of associated angiosperm trees (Brodribb et al., 2012). Many Fagaceae are well adapted to warm conditions, and generally have a less strict stomatal control and are able to maintain substantial transpiration levels during summer drought (Carnicer et al., 2013; Augusto et al., 2014).

Both Fagaceae and Pinaceae are showing signs of decline in some areas, including reduced growth, leaf area reductions, and increasing tree mortality (Carnicer et al., 2011; Rigling et al., 2013; McIntyre et al., 2015). Given the large functional differences between Pinaceae and Fagaceae, and the ecological importance of both families, the question of whether they will respond differently to ongoing climate change becomes highly relevant. Some reports suggest that contrasting trait syndromes between these families may be associated to different responses to recent changes in temperature in SW Europe, with positive growth responses to increases in temperature for Fagaceae but not for Pinaceae (Carnicer et al., 2013). Other studies, however, give more prominence to anthropogenic drivers, including historical changes in forest management and land use, in explaining recent forest dynamics in the same region (Vayreda et al., 2016).

Two important research questions emerge from the previous considerations: (1) are the dynamics of replacement of Pinaceae and Fagaceae observed in some European regions (Rigling et al., 2013; Vayreda et al., 2016) generalizable to other temperate regions worldwide? (2) what would be the ecological implications of this directional replacement, both in terms of ecosystem function (and provision of ecosystem services) and in terms of the future vulnerability of temperate forests to warmer and drier conditions? Here, we focus on the first of these two issues. We compiled a database of published studies analyzing the relative dynamics of Pinaceae and Fagaceae in temperate forests worldwide. We then analyzed this data to: (1) establish whether there is a consistent directional trend in recent decades towards greater abundance of Fagaceae relative to Pinaceae species in temperate forests worldwide, and whether this trend has led to a change in the dominant tree family in these forests; and (2) determine whether these changes are associated to specific conditions or certain geographic regions, reflecting differences in climate, historical forest management or land use.

2. Methods

2.1. Bibliographic review

A systematic review was performed at the global scale using bibliographic data available from the Web of Knowledge (http://apps.webofknowledge.com, accessed 28th February 2018). We targeted peer-reviewed journal articles on the comparative dynamics of Pinaceae and Fagaceae species in temperate forests worldwide. The following search terms were used, which include all genera in the two families studied: ((*Castanea* OR *Castanopsis* OR *Chrysolepis* OR *Fagus* OR *Lithocarpus* OR *Notholithocarpus* OR *Quercus* OR *Trigonobalanus*) AND (*Pinus* OR *Cedrus* OR *Cathaya* OR *Picea* OR *Pseudotsuga* OR *Larix* OR *Pseudolarix* OR *Tsuga* OR *Nothotsuga* OR *Keteleeria* OR *Abies*) AND (forest$) AND (dynamics OR succession OR regeneration OR recruitment) AND (survey$ OR substitution OR replacement OR change $)). This literature survey approach is complementary to studies using consolidated datasets such as those obtained from national forest inventories, which have already been used for similar purposes in some regions (e.g., Vayreda et al., 2016). Clearly, forest inventories provide more systematic and comparable experimental designs and data collection protocols. However, they are only available for a small and biased fraction of the world's forests, they tend to cover relatively short periods of time, they are not easily integrated across countries, and they offer limited information on potential drivers of vegetation change. A systematic literature survey as the one conducted here has the potential to overcome some of these limitations.

We included studies written in English or other languages (with English abstract). This search resulted in a total of ~1250 papers. The initial list of papers was then filtered according to the following criteria: (i) studies concerned "natural" vegetation (forest plantations and modeling studies were excluded), (ii) Pinaceae or Fagaceae were dominant (in terms of stem density or basal area) at the beginning or the end of the study period, (iii) the study period was well-defined, with clear dates for initial and final vegetation surveys, (iv) changes in vegetation were assessed between 1850 and 2016, (v) the study period was longer than three years, (vi) the study measured or made some inference on vegetation changes by species or groups of species using a quantitative measure of abundance (e.g., basal area, stem density, distribution area), and (vii) both families were clearly represented at the beginning or at the end of the study period (studies were removed when the proportion of Fagaceae relative to (Fagaceae + Pinaceae) remained $< 5\%$ or $> 95\%$ throughout the study period).

We obtained a final list of 51 papers matching these criteria. Since many of these papers included more than one study area, we considered unique combinations of paper by study area as our basic study unit ($N = 121$). The source of variability associated to the paper level in the hierarchical structure of the dataset was accounted for in our statistical analyses (see below). One of the studies (Vayreda et al., 2016) provided a synthesis of forest inventory data for Spanish forests. Since this was not directly comparable to the other datasets included in our analyses, which typically represented much smaller areas, we splitted the original dataset used in Vayreda et al. (2016) by administrative region, giving 12 different study cases.

The following information was recorded from the original papers for each of the study units (the complete dataset is given in Table S1, Electronic Supplementary Material): complete reference; geographic location (country, state or region, geographic coordinates); characteristics of the study area (vegetation type, dominant species); method used to assess vegetation change (permanent plots, forest inventory, aerial photography, satellite images); area covered by the study (i.e., total area sampled) (ha); baseline year; end date of the study; main drivers of vegetation change during the study period; type of variable used to quantify abundance; and the initial (baseline) and final value of the abundance variable for Pinaceae and Fagaceae, combining all values for the species belonging to each family.

The variables that were used to quantify abundance were: basal area (in $m^2\,ha^{-1}$ or % of total basal area, $N = 60$ study cases), stem volume (in $m^3\,ha^{-1}$ or % of total stem volume, $N = 23$), tree density (in stems ha^{-1}, $N = 20$), importance percentage (Choung et al., 2004; Lee et al., 2012; Jang et al., 2013) ($N = 12$), and distribution area (in ha or %, $N = 6$). When more than one of the previous variables was reported in a paper, the variables were prioritized in the same order given above and only the first one was considered. Drivers of vegetation change, as specified by the authors of each study, were classified in the following four categories: climate stress (e.g., temperature, drought), natural disturbances (e.g., wildfires, pests and pathogens, windstorms), direct anthropogenic disturbances (e.g., fire suppression, forest management, grazing), and successional dynamics in the absence of major disturbances.

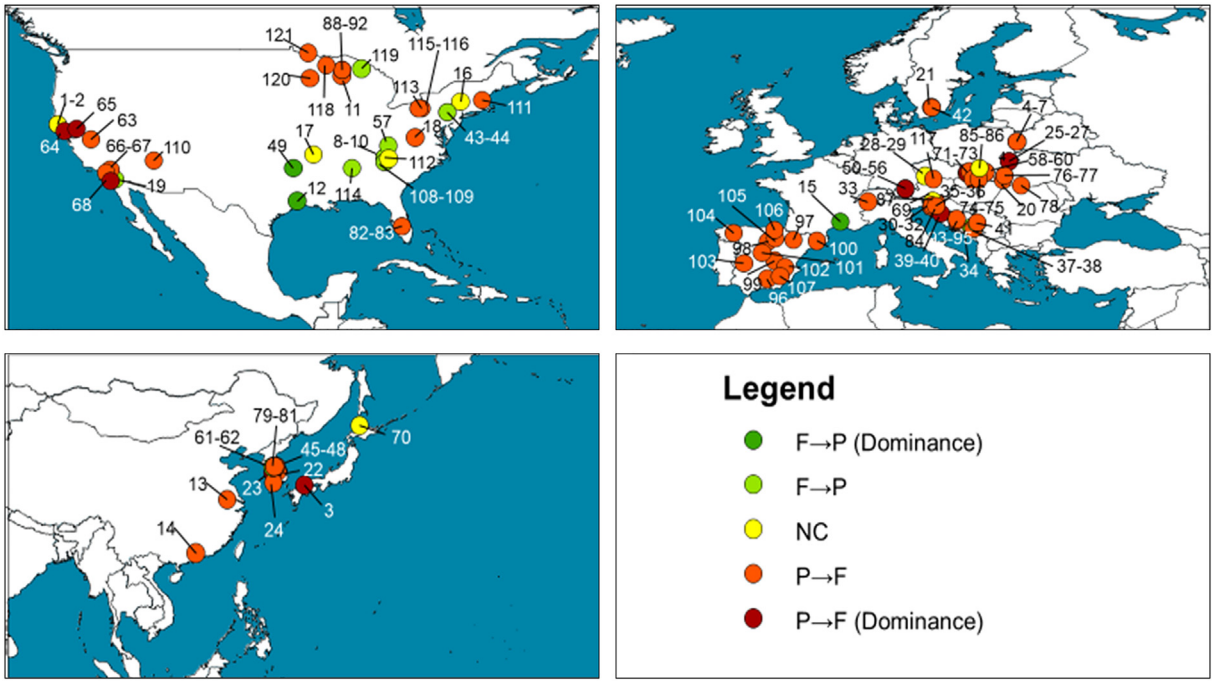

Fig. 1. Approximate locations of the 121 case studies of relative Pinaceae vs Fagaceae dynamics included in the study. Different colors indicate the direction of vegetation change (F- > P indicates increased Pinaceae abundance; P- > F indicates increased Fagaceae abundance; and NC denotes no change in the relative abundance of the two families, $|C| < 0.025$). Darker green or red colors indicate changes in dominance (see text for details). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.2. Assessing vegetation change

Changes in relative abundance between Pinaceae and Fagaceae were assessed using the following index of change (C):

$$\text{Index of change} = \frac{A^F_{end}}{(A^P_{end} + A^F_{end})} - \frac{A^F_{ini}}{(A^P_{ini} + A^F_{ini})}$$

where A refers to the value of the measure of abundance; the super-indices F and P denote Fagaceae and Pinaceae, respectively; and the sub-indices *end* and *ini* indicate the values at the end and at the beginning of the study period, respectively. A positive value of index of change indicates that Fagaceae abundance increases more (or decreases less) relative to Pinaceae (P → F), whereas a negative value indicates the opposite (F → P) and $C = 0$ indicates identical changes in the two families (no change, NC). Besides using this quantitative index of change, in some analyses we also used the corresponding categorical variable with three levels: Pinaceae to Fagaceae (P → F), Fagaceae to Pinaceae (F → P), and no change (NC). As low values of $|C|$ indicate very small relative changes that are unlikely to be biologically meaningful, we compared different threshold values of $|C|$ to determine which cases corresponded to the no change situation (NC), including 0.02, 0.025 and 0.03 (the overall distribution of C ranged between −0.6 and 0.5, with mean = 0.077 and median = 0.074). Results were identical in all cases and thus we only report those using $|C| = 0.025$ as a threshold. We also assessed when changes in the abundances of the two families led to changes in overall dominance. A change in dominance occurred when the family with the highest abundance (Pinaceae or Fagaceae, measured as described above) changed between the beginning and the end of the study period.

2.3. Climate data

To complement the data extracted from the articles, we also obtained total annual precipitation (L m^{-2}) and mean annual temperature (°C) using the geographic coordinates of each study site, as given in the original papers. These additional data layers were obtained from WorldClim Weather-Global climate data (30 arc-seconds resolution) for current conditions 1950–2000 (http://www.worldclim.org/current).

2.4. Data analysis

We used chi-square tests to assess whether there was a preferential vegetation change (P → F vs. F → P, excluding NC) globally or for each main region (corresponding to continents except in the case of North America, which was splitted between Eastern and Western territories). We also tested whether dominance changes were more frequent for sites initially dominated by Fagaceae or Pinaceae.

Classification trees are a statistical modeling technique to determine a set of conditions (from a set of explanatory variables) that allow accurate classification of cases in relation to a discrete response variable (De'ath and Fabricius (2000), and were used here to determine which variables were associated to different directions of vegetation change (the response variable, with three discrete classes: P → F, F → P and NC). Explanatory variables included total annual precipitation, mean annual temperature, driver of change, region and type of variable used to quantify abundance. This latter variable was included to account for potential methodological effects associated to the way abundance was assessed in each study.

Finally, a mixed-effects model was fit with the quantitative index of change as response variable and total annual precipitation, mean annual temperature, driver of change, region, type of variable used to quantify abundance, and length of the study period (in years, ranging from 3 to 159 years) as explanatory variables. Preliminary analyses showed that the effect of the size of the study area was not significant ($r = -0.09$, $P = 0.34$) and, since this variable was unavailable for a few case studies, we decided not to include it in the final model. Study was included as a random factor in the model to account for the fact that many of the studies (papers) included in our dataset contained more than one study case, which likely shared common experimental conditions and thus were not independent. Both the response variable (index of change) and the model residuals were approximately normally distributed. Significant differences were accepted whenever

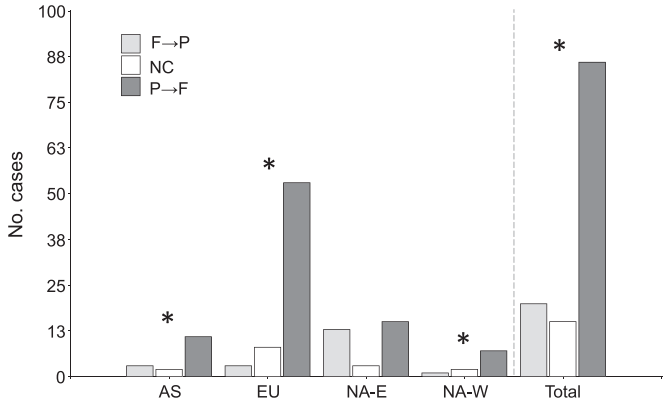

Fig. 2. Number of study cases by direction of vegetation change (F- > P indicates increased Pinaceae abundance; P- > F indicates increased Fagaceae abundance; and NC denotes no change in the relative abundance of the two families, $|C| < 0.025$) worldwide and by region (AS: East Asia, EU: Europe, NA-E: East North America, NA-W: West North America). An asterisk indicates significant differences between directions of change (F- > P vs P- > F), globally and by regions.

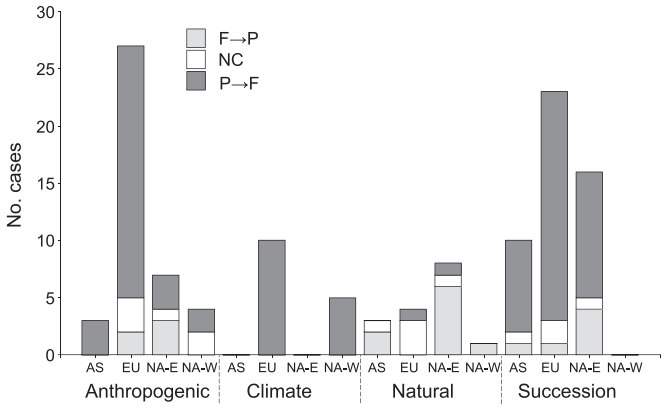

Fig. 3. Number of study cases by direction of vegetation change as a function of region (AS: East Asia, EU: Europe, NA-E: East North America, NA-W: West North America) and driver of change (Anthropogenic disturbances, Climate stress, Natural disturbances or Succession; see text for details). F- > P indicates increased Pinaceae abundance, P- > F indicates increased Fagaceae abundance, and NC denotes no change in the relative abundance of the two families ($|C| < 0.025$).

P < 0.05. All analyses were conducted using the R software environment (v.3.4.3, The R Project for Statistical Computing).

3. Results

The 121 cases obtained were distributed throughout the northern hemisphere, with 64 cases in Europe, 31 in East North America, 10 in West North America and 16 in (East) Asia (Fig. 1). Of those, 71% corresponded to changes in the relative abundance from Pinaceae to Fagaceae (P → F), 17% corresponded to the change from Fagaceae to Pinaceae (F → P) while 12% of the cases did not show clear changes (NC). Changes from Pinaceae to Fagaceae were significantly more frequent than the opposite trend, both globally (P < 0.001) and in all regions except East North America (P < 0.001 in Europe, P = 0.032 in (East) Asia, P = 0.034 in West North America and P = 0.705 in East North America) (Fig. 2). These changes in relative abundance, however, have not lead to significant changes in dominance in neither Pinaceae nor Fagaceae forests (P ≥ 0.05 in all cases).

The distribution of drivers of change differed among regions, with anthropogenic disturbances and successional dynamics being particularly common in Europe, successional dynamics being also common in (East) Asia and East North America, and natural disturbances being also common in East North America (Fig. 3). No obvious association was observed between the direction of vegetation change and climate, defined by total annual precipitation and mean annual temperature (Fig. S1, Electronic Supplementary material).

The classification tree results indicated that the only explanatory variable that was retained in the model (out of annual precipitation, temperature, driver of change, region and type of variable) was the driver of change. This variable alone allowed a reasonably good classification of the direction of vegetation change, with natural disturbances being associated to relative increases in Pinaceae or no changes (88% of cases within that group corresponded to F → P or NC) and all the other drivers being associated to increased Fagaceae abundance, the most common outcome (80% of cases within that group corresponded to P → F dynamics) (Fig. 4).

The analyses using the (quantitative) index of vegetation change largely confirmed the results obtained for the discrete variable categorizing the direction of vegetation change. Positive average values of the index of change, indicating preferential P → F dynamics, were observed in all combinations of region and driver of change except for natural disturbances in East North America and Asia, and anthropogenic disturbances in East North America (Fig. 5). The mixed-effects

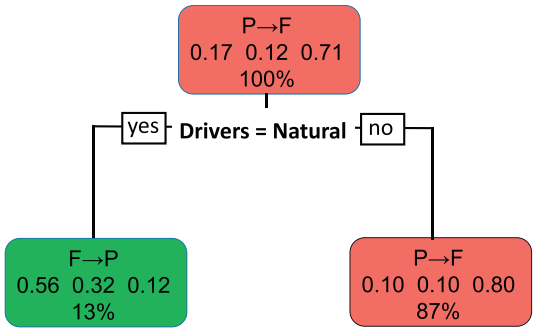

Fig. 4. Classification tree with direction of vegetation change as response variable (F- > P: increased Pinaceae abundance, P- > F: increased Fagaceae abundance) and driver of change as the only significant explanatory variable. The numbers indicate the proportion of cases in each category that correspond to each direction of vegetation change (in the order: F- > P, no change, P- > F) and the overall percentage of cases in each category.

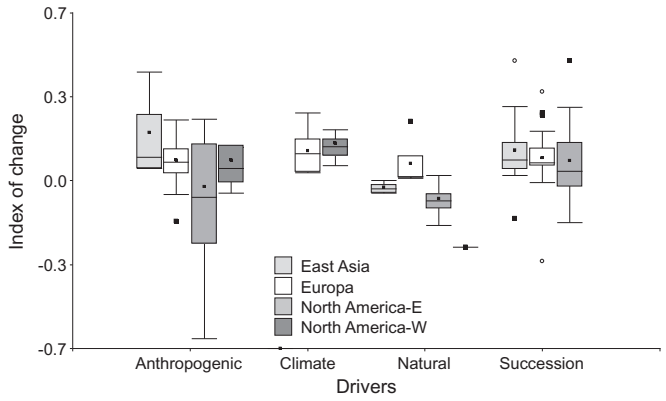

Fig. 5. Index of change (*C*) as a function of driver of change and region. A positive value indicates that Fagaceae abundance increases more (or decreases less) relative to Pinaceae (P → F), whereas a negative value indicates the opposite dynamics (F → P) and C = 0 indicates identical changes in the two families. The horizontal line and black dot inside the box give the median and the mean, respectively, the edges of the box are the lower and upper quartiles, the two whiskers extend up to 1.5 times the interquartile range from the top/bottom of the box, and the dots beyond the end of the whiskers represent outliers.

Table 1
ANOVA table for the linear mixed-effects model predicting index of change (*C*) as a function of type of variable used to assess abundance, region, driver of change, mean annual temperature, annual precipitation, and length of the study period.

Variable	Numerator degrees of freedom	Denominator degrees of freedom	F-value	p-value
(Intercept)	1	64	38.40	< 0.0001
Type of variable	4	43	1.87	0.1325
Region	3	43	3.65	0.0197
Driver of change	3	64	5.50	0.0020
Temperature	1	64	1.04	0.3116
Precipitation	1	64	2.54	0.1157
Study period	1	64	2.31	0.1335

model allowed us to assess the statistical significance of the previous patterns, and showed that the only two variables with a significant effect on the index of change (*C*) were driver and region (marginal $R^2 = 0.28$) (Table 1). Natural disturbances were the only driver of change for which the model predicted negative *C* values on average (using least-squares means estimation), implying preferential F → P dynamics. Predicted *C* values were significantly lower for natural disturbances than for climate stress and successional dynamics ($P < 0.05$), whereas anthropogenic disturbances showed intermediate values. Regarding region effects, predicted *C* values were all positive, but were significantly higher for (East) Asia than for Europe or East North America ($P < 0.05$). The effects of variable type, length of the study period, and precipitation and temperature climatology were not significant (Table 1).

4. Discussion

We report a generalized increase in Fagaceae species at the expense of Pinaceae in temperate forests, particularly in Europe and (East) Asia. The patterns are less clear in East North America, which is associated to a different dominant driver of vegetation change in this region (see below). These prevailing P → F dynamics were not significantly affected by the length of the study period. This result suggests that compensatory dynamics (which could promote stability in the long term, Lloret et al., 2012) were not a dominant factor explaining the observed vegetation changes, although they were observed in some cases. For instance, forest composition in central Massachusetts experienced a variety of successional stages ranging from late-successional *Tsuga canadensis* assemblages to assemblages dominated by early successional to mid-successional taxa such as *Castanea*, *Quercus*, and *Pinus*; but with similar relative abundances of Pinaceae and Fagaceae at the beginning and end of the study period (McLachlan et al., 2000).

Our results show that there is a directional change from Pinaceae to Fagaceae in most forests worldwide and, in particular, in areas where vegetation dynamics are driven by climatic stress, successional dynamics and, to a lower extent, (direct) anthropogenic disturbances. This directional pattern disappears in areas where natural disturbances drive vegetation change. The higher frequency of F → P dynamics under natural disturbance regimes is consistent with the fact that many Pinaceae, particularly those belonging to the *Pinus* genera, are considered early-successional species (Vayreda et al., 2016; Searle and Chen, 2017). A similar argument explains why the opposite, P → F change dominates areas driven by natural succession. It is less clear why anthropogenic and climate-driven disturbances may promote Fagaceae at the expense of Pinaceae. Possible explanations are that the legacies from past anthropogenic disturbances and climate warming directly contribute towards the observed composition changes. For example, in some areas of Europe, the replacement of firewood (obtained mostly from Fagaceae) by fossil fuels has indirectly promoted broadleaves (Vayreda et al., 2016). Also in Europe, less intense forest management and abandonment of lands formerly used for cultivation or grazing has resulted in successional dynamics towards forests increasingly dominated by Fagaceae, particularly *Quercus* species (Rigling et al., 2013; San Roman Sanz et al., 2013; Morales-Molino et al., 2017). In SW North America, changes in fire regimes since European settlement have also led to an increase of Fagaceae (*Quercus* species) relative to Pinaceae in *Pinus ponderosa* forests (Fulé et al., 1997).

Despite the fact that our simplistic analysis did not detect any effect of average climate on the observed vegetation dynamics, it is likely that climate extremes have a role in the observed patterns, at least in some areas. Increased temperature and drought has been associated with forest mortality episodes, in many cases affecting Pinaceae species, whereas Fagaceae appear less affected (Gimmi et al., 2010; Ruiz-Benito et al., 2013; Carnicer et al., 2014; McIntyre et al., 2015; Mcdowell et al., 2016). In a recent global synthesis, drought legacy effects on radial growth have been reported to be more prevalent in Pinaceae relative to Fagaceae (Anderegg et al., 2015), possibly reflecting different strategies to face drought stress (Ruiz-Benito et al., 2014; Anderegg et al., 2016; Cailleret et al., 2017). Although these latter results pertain only to growth responses, radial growth dynamics and tree mortality are tightly associated (Cailleret et al., 2017). Finally, the high recruitment capacity of most Fagaceae likely confers them an additional advantage (relative to Pinaceae) in face of disturbance (e.g., Eugenio and Lloret, 2004; Carnicer et al., 2014; Abrams et al., 2017).

Several factors likely explain why changes towards increased dominance of Fagaceae were less clear in East North America compared to Europe and (East) Asia. Firstly, our own results indicate that natural disturbances appear to be a particularly important driver of vegetation change in this region, and this is the only type of disturbance not associated to P- > F dynamics. This would be consistent with the view of Pinaceae as relatively early-successional species compared to Fagaceae. In addition, late-successional Pinaceae species (e.g., many *Abies*, *Picea* and *Tsuga* species, as opposed to relatively early-successional *Pinus*) are particularly common in North America, which could also cause increased Pinaceae as a result of successional dynamics in this region (Chen and Luo, 2015; Searle and Chen, 2017). Finally, many of the recent changes in forest management and land use that have promoted broadleaves in Europe (e.g., land abandonment) have not been observed (or are much more recent) in North America (Paulson et al., 2016; Copes-Gerbitz et al., 2017). Although not captured in our literature review, Pinaceae encroachment upon savannas and woodlands formerly dominated by Fagaceae have been also observed in NW North America, mostly associated to changes in fire frequency, introduction of exotic species, and grazing intensification (Gedalof et al., 2006; Devine and Harrington, 2013; Copes-Gerbitz et al., 2017).

The fact that Fagaceae and Pinaceae have contrasted functional traits (Brodribb et al., 2012; Carnicer et al., 2013; Ruiz-Benito et al., 2017) implies that the observed changes in the relative abundance of the two groups may have important implications for ecosystem function and the provision of forest ecosystem services (Vayreda et al., 2016). Possibly even more important are the implications of these compositional changes in terms of future forest resilience to ongoing climate change. On one hand, conifers in general and Pinaceae in particular are frequently considered more capable to withstand extreme abiotic stress (e.g. Coomes et al., 2005) and, in relation to drought stress, tend to operate with wider hydraulic safety margins than angiosperms (Choat et al., 2012). On the other hand, some attributes, including higher resprouting capacity, may favor Fagaceae under warmer and drier climates (Carnicer et al., 2013). Palynological evidence shows that oaks (Fagaceae) have indeed increased in abundance during warm interglacial periods, at least in some regions (McIntyre et al., 2015). However, the net result of all these contrasting responses remains highly uncertain.

In conclusion, we report a widespread increase in dominance of Fagaceae species at the expense of Pinaceae across northern temperate forests, with the exception of Eat North America. Although our results

appear consistent and summarize, to the best of our knowledge, all published reports worldwide, we acknowledge that the number of case studies on which we base our synthesis is low and possibly not representative at the global scale, as large areas of the temperate forest biome are not well represented (e.g., most of the Asian continent, NW North America). The driver of vegetation change emerges as an important factor determining the direction of observed vegetation dynamics, with transitions from Pinaceae to Fagaceae dominating in all cases except for natural disturbances. Different disturbance histories, as well as differences in regional floras, likely determine the dominant direction of vegetation transitions in different temperate regions. If the pattern of directional change observed here proves to be general for the temperate biome, the potential implications for ecosystem function and forest resilience are large and clearly deserve further study.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gloplacha.2018.04.001.

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